BENTHIC SALT MARSH ALGAE AT IPSWICH, MASSACHUSETTS[1]

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This paper is the first of a two-part study of the attached algae of the Ipswich salt marsh. Here, emphasis is placed on the occurrence, periodicity, and morphology of the benthic algae. A second paper will describe in detail the ecology of the marsh algae at Ipswich.

In previous botanical investigations of salt marshes, studies of seed plants far exceed those of other plant groups. For the New England area we can refer to Chapman's (1939, 1940) studies of the Saugus (Massachusetts) marsh in which he emphasizes flowering plants. More recently, Blum (1968) demonstrated the interrelationships between salt marsh Spartinas and their associated benthic algae. Summaries of the few papers which deal with the New England salt marsh flowering plants are presented by both Chapman and Blum.

On the other hand, considerable attention has been focused on the extensive marshes of the southern and southeastern Atlantic coast. Pomeroy (1958, 1959), Schelske & Odum (1961), and Odum (1961) contributed much with respect to our knowledge of community structure and overall productivity of the southern tidal marshes. Similar studies in orientation and details have not been attempted in New England salt marshes.

Unlike the salt marsh flowering plants, the attached algae of these eco-systems remains a poorly developed focus of research, whether in the Gulf and southeastern United States or in New England. Chapman (1960) summarized the literature dealing specifically with marsh algae, convincingly demonstrating the need for long range studies of these little understood but important plants.

Doubtless, by far the greater number of benthic marine algal species found in New England salt marshes are rep-

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[1]Revised portion of a Ph.D. thesis, of senior author, University of Massachusetts.

resented in Taylor (1957). Taylor's treatment, however, presents but a stylized description of these species and the briefest account of their occurrence. The greatest source of omission in this flora lies not with the macroscopic algae, but with the numerous minute forms which can be determined only through careful microscopic examination. Of these forms, the attached chrysophytes and haptophytes undoubtedly contain the largest number of species new to our area and new to science. Nonetheless, Taylor (1957) is our point of departure for phycological literature pertaining to the salt marshes of the northeast.

Salt marshes are low areas immediately landward to a coast or embayment. The seaward portions of the marsh are inundated periodically by full strength seawater, with the more peripheral landward extensions being subject to freshwater inflow. Commonly, marshes are strongly dissected with tidal creeks of varying sizes, which result in a more rapid mixing of marine and freshwater. Thus, the salt marshes are unique, well defined environments characterized by gradients in salinity, temperature, pH, tidal amplitude, and are rarely exposed to waves of any size.

Tidal marshes are deceivingly homogeneous in appearance with respect to their macroscopic vegetation, being dominated by species of *Spartina* (*S. alterniflora* var. *glabra*, *S. patens*, and *S. pectinata*) and various members of the Chenopodiaceae (*Atriplex*, *Suadea*, and *Salicornia*). The *Spartina* grasses are particularly important in that they bind the predominantly loose organic substratum of the marsh, add to this substratum through senescence and decay, and, in part, bring about changes in its composition. The seed plants, however, represent but a small fraction of the total number of marsh plant species, if one includes the attached algae; by far the greater number of species present belong to the algae. Owing to their relatively small size in relation to the flowering plants, the algae are invariably overlooked unless one makes an effort to search them out. Small they may be, but because of their large numbers and frequently sharp seasonality, the marsh sur-

face takes on distinctive and different subtle hues owing largely to the periodicities of these plants.

Salt marshes are of further interest in that their biological features are directly related to and result from the distinctive physical and chemical characteristics of the marsh. The attached alga constitutes a highly appropriate tool of research for the study of biological adaptation to continuous changes of virtually all of the environmental factors present in the marsh. Owing largely to their small size, populations of marsh algae may be grown easily and rapidly in culture. Studies of the control of the initiation, formation, and discharge of sexual and asexual reproductive cells can be achieved using selected taxa of marsh algae. Growth rates and initial development as affected by different degrees or combinations of different environmental factors can be studied *in vivo* and relationships drawn with comparable situations in the natural environment. Moreover, the characteristically sheltered environment of the marsh, unlike that of the open coast or the sublittoral, makes more feasible long lasting experiments under natural conditions which may parallel or supplement experiments under the controlled conditions of the laboratory. We propose that the salt marsh environment and the salt marsh algae offer many opportunities for the phycologists interested in experimental ecological investigations. In our experiences, the salt marsh environment is a fascinating and fruitful area . . . many questions remain to be discovered concerning the marsh biota, and still more remain to be answered.

The conspicuous mud flats and meadow-like expanses of marshland in and surrounding the Ipswich area comprise approximately 10% of the total salt marsh acreage in Massachusetts (Mass. Dept. Nat. Res., 1964). Here, the salt marsh acreage adjacent to the Castle Neck River, Ipswich, Mass., was chosen for an intensive botanical investigation. The Castle Neck River and its system of tidal creeks constitute a true estuarine environment.

Following a 13 month study of the algal vegetation of the Ipswich marsh, 5 stations were selected as representing

a habitat range and, in all probability, close to total algal diversity within the entire marsh system. Collections from these stations were made at a minimum of fortnightly intervals from September, 1963, through December, 1964. Each station was delimited by a line transect 1.5 m wide and of varying length depending on physiognomy of the station.

Positions of the 5 stations chosen for this study are indicated in Fig. 1; a few comments concerning the character of these stations are appropriate: **Station 1:** typically marine, little influenced by freshwater runoff; shoreline a vertical mud bank; substrates of mud, rocks, small stones, and phanerogams. **Station 2:** similar to Station 1, but a

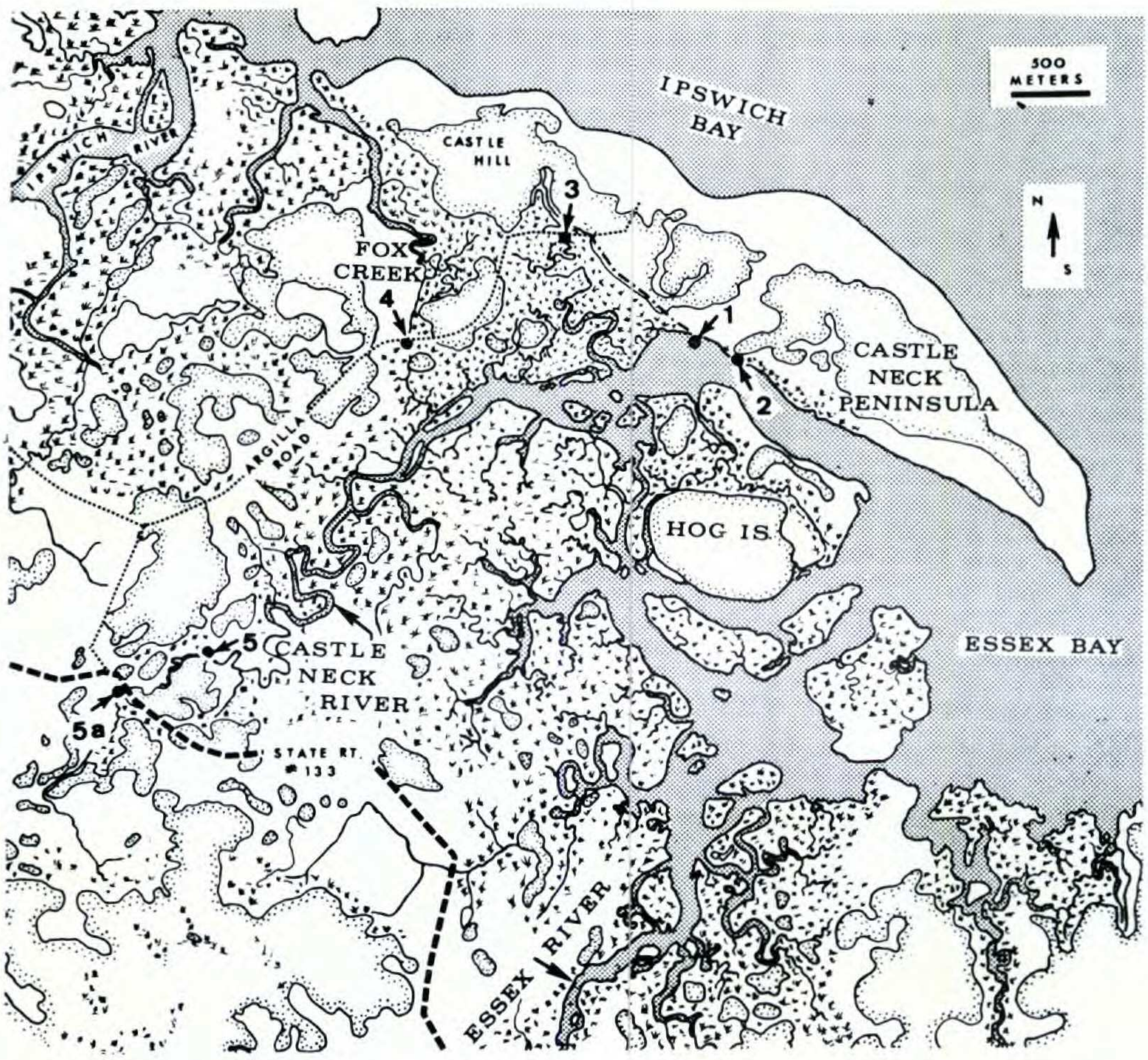

Fig. 1. Location of stations studied at the Ipswich Marsh. Land of highest elevation is enclosed by solid lines and stipple.

more gently sloping shore; substrates predominantly rocks, small stones, *Modiolus demissa*, and phanerogams. **Station 3:** tidal ditch outflow 0.3-1 m deep, seasonally influenced by freshwater runoff; substrates of small stones and wood pilings. **Station 4:** sector of a tidal creek beneath a bridge spanning Fox Creek 1.6 klm west of Station 3; 1.5 m of water at high spring tides, essentially dry at low water level; deeply shaded; substrates of small stones, shells, and wood pilings. **Station 5:** consists of two substations, 5*a* and 5*b*: Substation 5*a*-transect through a major tidal creek which runs under Northgate Rd. (intersect with State Rt. 133) at the head of the marsh; 0.6 m at high water and a variable cover of freshwater at low tide; substrates of small stones, mud, and the phanerogam *Ruppia maritima*. Substation 5*b*-differs from 5*a* in the prevalence of a mudsilt substrate, continuous deep water [ca. 0.6 m] coverage, and its slow movement of water downstream.

Fortnightly measurements were made of salinity, water temperature, and pH at each station. Because these parameters change continually in an estuarine area, their patterns of seasonal fluctuations and their extremes more accurately characterize each station than do average values. Ranges in salinity, water temperature, and pH are presented in Table I.

Table I. Salinity, Temperature, and pH Ranges

Stations	Salinity Range (0/00)	Temperature Range (°C.)	pH Range
1, 2	18 - 33	-1.5 - 24	7.3 - 8.0
3	3 - 33	-2 - 27	6.7 - 8.0
4	13 - 32	3 - 23	7.2 - 7.8
5, a and b	0 - 27	0 - 25	6.4 - 7.4 (7.6)

The salinity systems of Rochford (1952) and the Venice System (1959) were used to characterize the water mass at each station. All salinity data indicate the station studies encompass a distinctly estuarine environment.

Algal cultures used in this study were grown in petri dishes containing Erd-Schreiber solution (Provasoli, et al., 1957), either full strength or diluted by 1/2 normal seawater depending upon the marine character of the environment from which the plants were collected. Cultures were maintained either at temperatures of 10-11°C or at 14-15°C under constant light; light intensities ranged from 50-200 f.c., as measured by a Weston Illumination Meter Model 756.

Species Tabulation and Comments

There are few papers that pertain strictly to the attached algae of New England tidal marshes; this paucity of information is particularly apparent in any phycological consideration of salt marshes of the Massachusetts coast. Our study tabulates the attached marine algae collected in the Ipswich marsh and also presents morphological, cytological, and life history details of some salt marsh algae which are incompletely understood or which have been unknown. In addition, we have attempted to make evident a variety of phycological problems which await future research.

CYANOPHYTA[2]

CHROOCOCCALES

Coccochloris stagnina Spreng.
Anacystis dimidiata (Kuetz.) Dr. & D.
Agmenellum quadruplicatum (Menegh.) Breb.

CHAEMOSIPHONALES

Dermocarpa olivaceus Crouan
D. violacea Crouan
D. prasina (Reinsch.) Born. & Thur.

HORMOGONIALES

Oscillatoria amphibia Ag.
O. subuliformis Kuetz.
Spriulina subsalsa Oersted.
S. major Kuetz.
H. glutinosum (Ag.) Gom.
H. holdenii Tilden
Schizothrix calcicola (Ag.) Gom.

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[2]Descriptions and ecological data for blue green species have been published previously (Webber, 1967).

Lyngbya aestuarii (Mert.) Lieb.
L. aestuarii var. *ferruginea* Gom.
L. lutea (Ag.) Gom.
L. semiplana (C. Ag.) J. Ag.
Symploca hydenoids Kuetz.
S. atlantica Gom.
S. funicularis Setch. & Gardn.
Hydrocoleum lyngbyaceum Kuetz.
Microcoleus chthonoplastes Thur.
M. tenerrimus Gom.
Nodularia harveyana (Thwaites) Thur.
Anabaena torulosa (Carm.) Lag.
Tolypothrix tenuis Kuetz.
Calothrix confervicola (Roth) Ag.
C. crustacea (Thur.) Fan
Rivularia atra Roth
R. nitida Ag.

Chlorophyta

Systematic treatment of the green algae follows that used by Taylor (1957), with several exceptions. For *Enteromorpha*, reference was made to Bliding (1938, 1944, 1963, 1968); for species of *Cladophora*, van den Hoek's (1963) scheme was adopted; for *Rhizoclonium*, Koster's (1955) revision was followed.

CHLOROCOCCALES

Codiolum gregarium var. *intermedium* (Fosl.) Collins

Endophytic through the year in leaves of *Spartina* grasses and *Glaux maritima*. Station 1.

Chlorochytrium moorei Gardn.

Endophytic in *Enteromorpha flexuosa* ssp. *paradoxa* in December. Station 1.

C. grande Bristol

Abundant in leaves of *Spartina patens* in October. Station 1.

ULOTRICHALES

Ulothrix flacca (Dillw.) Thur. in LeJol.

Attached to wood pilings, marsh grasses, and littoral fuci from December to early May, with zoospores through the winter and spring and isogametes in March. Stations 1, 2.

U. pseudoflacca Wille

Located from January through May mixed with *U. flacca*, zoospores produced through the spring, biflagellate

swarmers not seen. Stations 1-3, most abundant at Station 3.

U. subflaccida Wille

On wood pilings and stones from November through the winter to May, mixed with the two above *Ulothrix* species, only zoospores seen. Stations 1-3.

Pseudendoclonium submarinum (Reinke) Aleem & Schulz.

Collected throughout the year, but most luxuriant during the winter, from supralittoral wood pilings.

Cultures of this species from small clusters of cells yielded highly branched filamentous plants. Zoosporangia (Wille, 1901, figs. 124-126) were found in culture material, as were biflagellate swarmers, but discharge from sporangia was not seen. Fusion of motile cells is still to be described for this species.

Percursaria percursa (C. Ag.) Bory

This species was most abundant along the seaward marsh edge, from October through May, entangled with *Rhizoclonium riparium* in the Spartinetum alterniforetum. Stations 1, 2.

Bliding (1963) demonstrated sexual and asexual motile cells in this species; these were not seen from either field or cultured material of the Ipswich plants.

Capsosiphon fulvescens (C. Ag.) Setch. & Gardn.

At the Ipswich salt marsh, this species is represented by two populations which are morphologically, spatially, and seasonally distinct. Plants 10 cm long by 1 mm wide were collected from an upper littoral marsh depression at Station 1 (April through June), their occurrence coinciding with a salinity range of between 18-30o/oo. By contrast, plants of *C. fulvescens* having a maximum length of 1 cm and a width varying from 24-68 μ (maximum of 90 μ, occurred on small stones at the extreme head of the marsh (Substation 5a, August through December); during this time the salinity ranged from 2-20o/oo.

Capsosiphon fulvescens is clearly a euryhaline species. Do major salinity changes alone or in combination with other environmental factors control its gross morphology

at Ipswich? Or are we, perhaps, dealing with two genetically distinct populations of this species? Waern (1952) and Bliding (1963) also cite *C. fulvescens* as a euryhaline species, but do not make reference to form differences within the populations they studied. Another factor that may have some bearing on the grossly different development of the two populations at Ipswich is the lack of tidal emersion for the plants at Substation 5a and the normally occurring changes in tidal amplitude at Station 1. Additional studies of *C. fulvescens* involving both laboratory and field approaches are required before more can be said about plants of this taxon.

In our cultures, *Capsosiphon fulvescens* plants of both populations formed quadriflagellate zoospores which, after release from the parental cells, grew into erect thalli. On the other hand, Bliding (1963), in addition to finding quadriflagellate zoospores, reported biflagellate swarmers; he was unable to ascertain the function of these biflagellate cells. We have not obtained biflagellate swarmers from the Ipswich plants.

Enteromorpha

The morphological variations assumed by species of *Enteromorpha* in response to environmental conditions in large measure negate the value of growth habit as a diagnostic feature for species determination. Rather, cytological characteristics, such as cell size, shape, pattern of arrangement, plastid morphology, and number of pyrenoids appear to be more stable species criteria.

Because this genus has long been recognized as troublesome, our preliminary species determinations were sent to Dr. Bliding either for confirmation or reassignment; the species determinations given here are essentially those of Bliding.

Immediately below the seaward marsh edge at Station 1 there occurs a distinct band of green vegetation which we refer to as the "Enteromorpha facies" (Fig. 2); the species here include *Enteromorpha ahlneriana*, *E. intestinalis*, *E.*

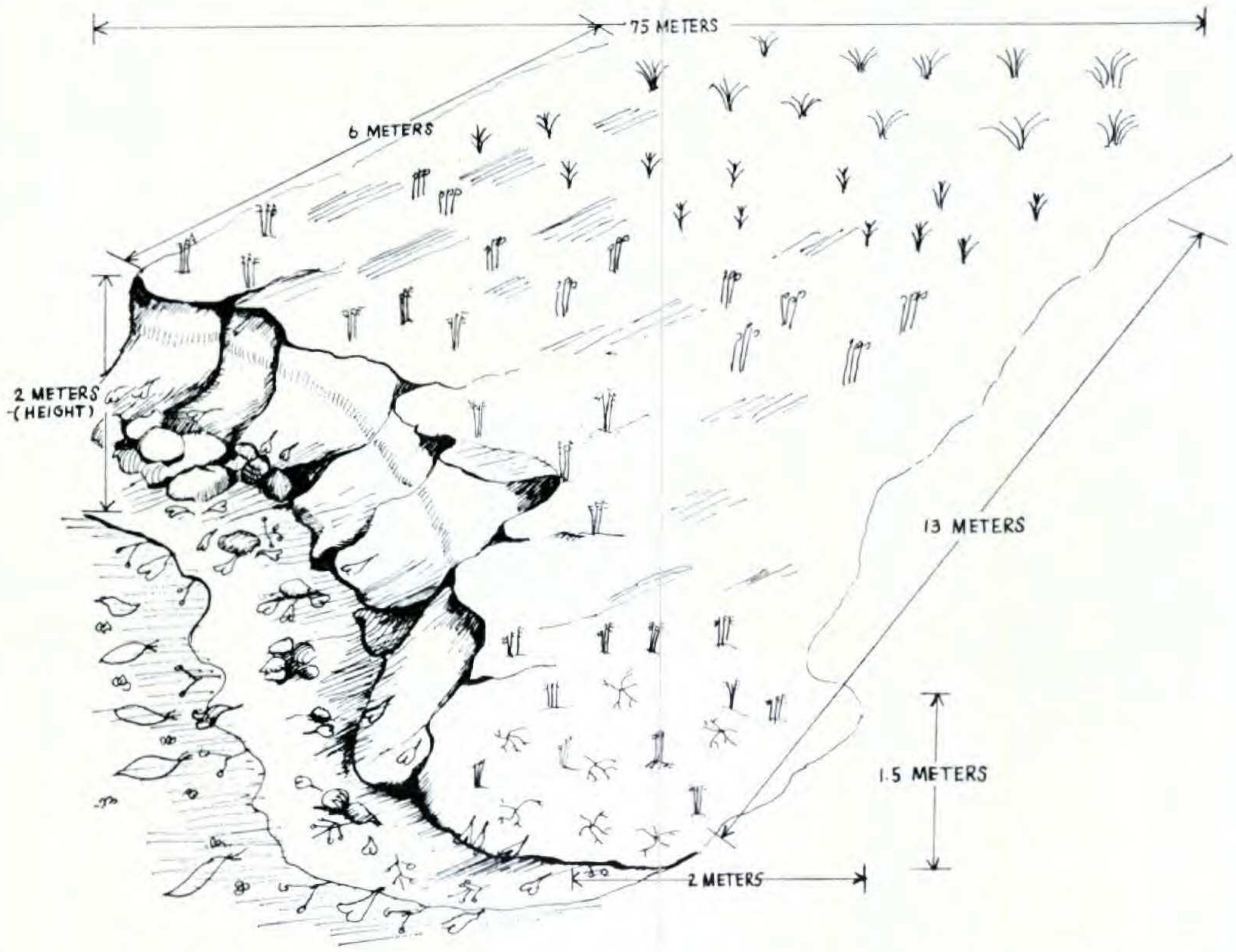

Fig. 2. A shore segment along the Castle Neck River indicating the *Enteromorpha* facies.

flexuosa ssp. *paradoxa*, and *E. prolifera*. By contrast, several other *Enteromorpha* species were located solely in the upper littoral zone, e.g., *E. ahlneriana* type II and *E. flexuosa* type III; still others were restricted to the sublittoral zone, namely *E. ahlneriana* type III, *E. clathrata*, *E. linza* (and var. *oblanceolata*), and *E. flexuosa* (ssp. *flexuosa* and ssp. *pilifera*). *Enteromorpha intestinalis* was the only *Enteromorpha* to be located in both sublittoral and upper littoral regions.

KEY TO ENTEROMORPHA SPECIES

a. Plants unbranched, or with small proliferations from the conspicuous stipe-like lower portion. b.

a. Plants highly branched. c.

b. Plants hollow throughout, cells commonly in 2's and irregularly placed, one pyrenoid per cell. . . . . *E. intestinalis*

b. Plants with the thallus fused in the mid region so that only the edges and stipe are hollow as seen in cross section, cells in longitudinal and horizontal rows, one pyrenoid per cell. . . . . *E. linza* var. *linza*
b. Thallus markedly expanded above, a plant of winter and early spring. . . . . var. *oblanceolata*
c. Plants repeatedly branched, branches tapering to the apex, cells rounded below and irregularly placed, in longitudinal rows above, 3-4 pyrenoids per cell. . . . . *E. clathrata* I
c. Plants branched, branches not tapering to the apex, cells in longitudinal rows throughout, pyrenoids mostly 1-3. d.
d. Pyrenoids 1 (2) per cell. . . . . *E. ahlneriana*
d. Pyrenoids mostly 2-4 (5) per cell.
e. Branches multiseriate, tips long and uniseriate, main axis cells with mostly 2-4 pyrenoids. . . . . *E. flexuosa* ssp. *flexuosa*
e. Branches mostly uniseriate, cells with 1-3 pyrenoids throughout. . . . . ssp. *paradoxa* III
e. Branches narrow, sharply distinct from the much broader main axis, cells with 3-5 pyrenoids. . . . . ssp. *pilifera*

E. ahlneriana Bliding

Plants to 14 cm long, with or without a distinct main axis, thalli to 1 mm wide, highly branched with branches either long and uniseriate or broad (to 1 mm) and tapering at the base, cells 8.6-18.6 μ × 12.4-31 μ, in longitudinal rows, one (rarely two) pyrenoid per cell. One group of plants of this species resembling Bliding's type II occurred throughout the year in the *Enteromorpha* facies. Station 1. A second population resembling Bliding's type III was collected from rocks and shells throughout the summer in the sublittoral. Stations 1 and 2.

E. clathrata (Roth) Grev. type I

Plants to 20 cm long, several orders of branching, main axis to 500 μ wide, branched to 220 μ diameter and ultimately tapering to 12.4-15 μ wide at the tips, cells 14-22 μ ×

11-31 μ, in a longitudinal series, 3-4 pyrenoids per cell. Attached to stones and *Fucus vesiculosus* during the summer in the sublittoral. Stations 1 and 2.

E. intestinalis (L.) Link var. *intestinalis*

Plants unbranched or slightly proliferating at the base, thallus expanded above the stalk-like base, 1 mm to 1 cm wide and to 50 cm long, cells 7.4-15 μ × 12.4-18.6 μ, occasionally to 24.8 μ, cells with rounded to angled walls in surface view and usually grouped in 2's, irregularly arranged, one pyrenoid per cell and the chloroplast not covering the cell face; thallus 19-25 μ thick in cross section with the cells 14.8-17 μ tall.

Two size classes of this species were evident during this study. One population consistently contained relatively small plants (to 7 cm) and collected through the year from the *Enteromorpha* facies. A second size class contained larger plants (to 50 cm) attached to stones and *Ruppia maritima* in Substation 5a and occurred only during the summer. The consistent size disparity between these two populations may be related to salinity differences for maximum growth of *E. intestinalis* at Ipswich appears inversely proportional to salinity levels. A similar relationship of plant size and salinities has been reported by Bliding (1963) for different populations of *E. intestinalis*. In August the *Enteromorpha* plants from Substation 5a released biflagellate, non-fusing swarmers. According to Bliding (1963) such swarmers may represent one half of a sexual strain, or they may function as zoospores, as apparently was the fate of these swarmers from Ipswich.

E. linza (L.) J. Ag. var. *linza*

Plants unbranched, to 1 cm wide and to 18 cm long, thallus blade-like and fused in the mid-region so that only the edges and stalk portions are hollow, as seen in cross section, cells 9-12.4 μ × 8.6-18.6 μ with thick, rounded walls, cells arranged in horizontal and longitudinal rows, one pyrenoid per cell; thallus 49-55 μ thick below and 62-68 μ thick above in cross section with the cells 10-17 μ wide and

31 μ tall; quadriflagellate zoospores released in September. Attached to small stones from June to October in the upper sublittoral. Stations 1 and 2.

var. *oblanceolata* Doty

Plants to 17 cm long, thallus markedly expanded above to 1.5 cm.; the plants 68 μ thick in cross section of the mid region, the cells here 14.8-18.6 μ diameter and 22-27 μ tall. Collected on small stones from February to April in the upper sublittoral. Stations 1 and 2.

E. flexuosa (Wulfen ex Roth) J. Ag. ssp. *flexuosa*

Plants to 35 cm long, highly branched, tips long and uniseriate but branches not markedly tapering, 25-37 μ wide, cells 12.4-15 μ $\times$ 12.4-31 μ, in longitudinal rows, 2-4 (5) pyrenoids per cell with 2 most commonly in the smaller branch cells. Attached to stones and *Fucus vesiculosus* during the summer in the sublittoral. Stations 1 and 2.

ssp. *paradoxa* type III (Dillw.) Bliding

Plants to 7 cm long, branches mostly uniseriate or at least with uniseriate tips, cells 12.4-21 μ $\times$ 24.8-31 μ, occasionally to 40 μ, cells arranged in horizontal and longitudinal rows, 1-3 pyrenoids per cell. This plant appears to be the *Enteromorpha plumosa* Kuetz. listed in Taylor (1957). Present throughout the year as a component of the *Enteromorpha* facies. Station 1.

ssp. *pilifera* (Kuetz.) Bliding

Plants to 30 cm long, "intestinalis-like" in appearance, narrow branches markedly distinct from the broader main or central axis, cells 12.4-17 μ $\times$ 11-24.8 μ, arranged in longitudinal rows but becoming unordered in large plants, the largest cells with angled edges, 4-5 pyrenoids per cell, but 3-4 in cells of the smallest branches. These plants strongly suggest *Enteromorpha prolifera* (Muell.) Ag. in Taylor (1957). Attached to submerged rocks and wood through the summer. Station 3, but occasionally located on stones in the sublittoral, Stations 1 and 2.

Enteromorpha sp.

Several other *Enteromorpha* species were collected from

the Ipswich salt marsh, these rarely and in small quantity. Before accurate species descriptions can be presented, we prefer to have more data from field collections and laboratory cultures. Tentatively, these plants, all recorded from Massachusetts for the first time, are *Enteromorpha prolifera* (Muell.) J. Ag. (ssp. *prolifera* Bliding and ssp. *gullmariensis* Bliding), and *Blidingia minima* Kylin.

Ulvaria oxysperma (Kuetz.) Bliding

Present as small plants (to 5 mm long) at the seaward marsh edge, October through June, Stations 1, 2. Larger plants (to 6 cm long) occurred on wood pilings, September to April, Station 3, and on small stones from September through December. Substation 5a.

Kornmanniana leptoderma (Kjellm.) Bliding

Plants commonly to 7 cm long, epilithic and epiphytic on algae, December to May, Stations 1, 2; epilithic from November to March, Station 4.

Ulva gigantea (Kuetz.) Bliding

Epilithic through the year in the sublittoral, most abundant during the summer. Stations 1, 2.

U. rigida (C. Ag.) Thur.

On submerged rocks and woodwork from June to November, zoospores in September. Station 3.

CLADOPHORALES

Chaetomorpha linum (O. F. Muell.) Kuetz.

Epilithic in the sublittoral through the year. Stations 1, 2.

C. melgonium (Web. & Mohr) Kuetz.

Collected as floating masses washed in among *Chondrus crispus*; doubtful as occurring as attached in the salt marsh. Station 4.

Rhizoclonium riparium (Roth) Harv.

Three forms are described from the Ipswich marsh; all three inhabit the marsh surface throughout the year, extending vertically from the *Spartinetum alterniflore-tum* landward to *Juncus gerardi*. Stations 1, 2.

f. *riparium* — filaments from 18.6-27 μ dia., rhizoidal

branches generally lacking, but if present, unicellular and short.

f. *validum* Fos. — filaments 31-62 μ dia., with or without rhizoidal branches.

f. *polyrhizum* Rosenv. — differing from f. *validum* by branching of the vegetative filaments, with rhizoids well developed and often multicellular.

R. implexum (Dillw.) Kuetz.

Filaments unbranched, 12.4-13.6 wide μ, cells 2-3 1/2 diameters long, occurring as entangled clumps beneath *Spartina patens*. Station 3.

Cladophora albida (Huds.) Kuetz.

Epilithic in the summer in the sublittoral, Stations 1 and 2, and as old and worn axes in January and September, Station 3.

C. sericea (Huds.) Kuetz.

On mid-littoral mud surfaces through the summer, Station 1, and as old and proliferating axes in tidal wash, Station 4.

The Ipswich plants are comparable with *C. flexuosa* (Muell.) Kuentz. (Söderström, 1963), and also with *C. glaucescens* (Griff.) Harv. and *C. crystallina* (Roth) Kuetz. in Taylor (1957).

C. vagabunda (L.) van den Hoek

Common in a drainage ditch during the summer, reduced to old (perenniating ?) axes in November, Substation 5b; also entangled with other algae, January and August, 1964, Station 3.

The Ipswich plants appear similar to *Cladophora expansa* (Mert.) Kuetz. in Taylor (1957).

C. liniformis Kuetz.

Entangled with other algae during the summer, Station 3, and washed ashore in September, Station 2.

SIPHONALES

Bryopsis plumosa (Huds.) C. Ag.

Attached to submerged rocks and wood from June to late December, the plants observed were always vegetative. Station 3.

PHAEOPHYTA

The systematics of the brown algae essentially follows the treatment used by Taylor (1957), with these exceptions: speciation in *Ectocarpus* follows Rosenvinge & Lund (1941) and Cardinal (1964); Powell's (1957) study is used for *Focus*; for *Laminaria*, see Wilce (1965); treatment of the Dictyosiphonales is after Papenfuss (1947).

ECTOCARPALES

Ectocarpus

The morphology of the plurilocular reproductive structures has been a widely used criterion to aid in determination of *Ectocarpus* species. However, one commonly encounters plurilocular organs whose morphology not only varies broadly within a given species, but also cuts across criteria used for species delineations. Examples of such variations are shown by Rosenvinge & Lund (1941, p. 19-20), Cardinal (1964, figs. 2-3), and in our collections of December, 1962 and those from August, 1963 to January, 1964. Therefore we choose to place less weight on the morphology of the plurilocular organ, thereby recognizing the following taxa from the Ipswich marsh:

E. confervoides var. *confervoides* (Roth) Kjellm.
Epiphytic on *Fucus vesiculosus* through the year, reproductive from October through December. Stations 1, 2.

E. confervoides var. *arcta* (Kuetz.) Kjellm.
Attached to plant debris in the *Enteromorpha* facies, seen only in October and November. Station 1.

E. confervoides var. *siliculosus* (Dillw.) Kjellm.
Epiphytic on coarse algae, April to July, plurilocular in May. Stations 1, 2.

E. confervoides var. *dasycarpus* (Kuck.) Rosenv. & Lund
Epiphytic on *Ruppia maritima* and on small stones, May to December, Substation 5a; epilithic from August through January, Station 3.

The Ipswich plants of this variety are considerably taller (10-12 cm), and have plurilocular organs approxi-

mately twice as wide (30 μ) and 2 1/2 times longer (to 660 μ) than previously reported (Rosenvinge & Lund, 1941; Taylor, 1957; Cardinal, 1964).

Giffordia sandriana (Zanard.) Hamel

Epiphytic on *Fucus vesiculosus* in the sublittoral zone, October and November. Station 2.

Pylaiella littoralis (L.) Kjellm.

At Ipswich, this species exists as two populations. One has plants highly branched, the old filaments wound into cord-like strands, epiphytic on *Fucus vesiculosus* in the sublittoral zone from July through December at Stations 1, 2. A second population consists of plants sparingly branched, with cells narrower and longer than the above, and occurs attached to plant debris in the *Enteromorpha* facies from December to March at Station 1. Plurilocular and unilocular reproductive organs were seen in both populations. Similar populations of *P. littoralis* distinct in morphology, vertical distribution, and seasonal occurrence have been reported from Great Britain (Russell, 1963).

Porterinema fluviatile (Porter) Waern

Epilithic on small stones, April, 1964. Substation 5a. (See Wilce, *et al.* 1970 b).

Ralfsia clavata (Harv. in Hook.) Crouan

Collected throughout the year on rocks in the sublittoral zone, sporangia from August to April. Stations 1-4.

R. verrucosa (Aresch.) J. Ag.

The location, seasonal occurrence, and reproductive periodicity for this species is the same as that for *Ralfsia clavata.*

Petroderma maculiforme (Wollny) Kuck.

Epilithic and on *Balanus* in the upper sublittoral from September to April, sporangia from October to April, Stations 1, 2; also, sparingly present on supralittoral wood pilings in January, the plants bearing sporangia, Station 3. (See Wilce, *et al.* 1970b).

Myrionema aecidioides (Rosenv.) Sauv.

Endophytic in the worn tips of *Laminaria saccharina,*

plurilocular organs from July through December, unilocular organs not encountered. Stations 1, 2.

DICTYOSIPHONALES

Petalonia fascia (O. F. Muell.) Kuntze

A dominant member of the winter algal vegetation, *Petalonia fascia* was first apparent from September to late October in the sublittoral and lower littoral at Stations 1-4; *P. fascia* disappeared from all localities by mid-June.

Only plurilocular organs were seen on the Ipswich plants of *Petalonia fascia*; fusion of motile cells released from these organs was not observed. When cultured, motile cells from plurilocular organs gave rise to filamentous plants which remained vegetative, in contrast to those described by Dangeard (1964) where unilocular sporangia developed on microthalli of *P. zosterifolia*.

Wynne's (1969) thorough study of *Petalonia fascia* from the California and Washington coasts demonstrates that blades of this species with plurilocular organs produce swarmers which grow into microscopic crusts. In turn, the crusts may bear unilocular sporangia, new erect blades, or both, depending upon culture conditions. Wynne did not observe fusion between motile cells from either blades or crusts. He suggests an asexual alternation in *P. fascia* which is facultative, with cool temperatures and short days favoring development of the blade stage, while warmer temperatures and long days induce crust formation.

On the basis of our observations, the most common life history pattern of *Petalonia fascia* in the Ipswich marsh appears to omit the crustose stage. A strict seasonality of thallus development occurs, the plants of which mature to form plurilocular organs. Swarmers from plurilocular organs develop into microthalli which ultimately give rise to erect blades by repeated vegetative divisions. Our field observations corroborate those of Wynne's from culture suggesting a light-temperature relationship for the initiation of new blades. While it is possible that the smallest crustose stages of *P. fascia* were overlooked at Ipswich, we prefer to believe the plants we studied did not possess the alternate

pattern of development involving the crusts and connecting filaments described by Wynne in California plants (1969), and Wilce in plants from West Greenland (1970a).

Scytosiphon lomentaria (Lyngb.) Link

A conspicuous winter dominant in the sublittoral and littoral, *Scytosiphon lomentaria* appeared at Ipswich in early September and persisted until the first week in May. This species was abundant at Stations 1, 2, and sparingly present at Station 3.

At the Ipswich marsh, *Scytosiphon* exists as two morphologically and spatially distinct populations, overlapping in their seasonal occurrence; we have referred to these as population "a" and population "b". Population "a" consists of plants to 35 cm tall, attached to stones and shells in the upper sublittoral and lower littoral. The plants had plurilocular reproductive structures from September to early May. Population "b" is composed of dwarf plants having a maximum length of 7 cm, no constrictions in the cylindrical thalli, and attached to plant debris and mud along the seaward edge of the marsh at Stations 1, 2. Plurilocular organs were formed in March and persisted through early May, soon after which this population was no longer evident on the marsh.

The problems encountered in attempting to interpret the life history of *Scytosiphon lomentaria* are similar to those already discussed in *Petalonia fascia*, i.e., the lack of sexuality, the apparent loss of the gametophyte phase, and the repeated formation of tubular, erect plants developing from microthalli. Culture conditions used to grow isolates of *Scytosiphon* were not varied, but under the uniform conditions previously described the following developments occurred. Motile cells from both "a" and "b" populations gave rise to microthalli; microthalli formed pluricular sporangia from which zoospores repeated the filamentous generation. Eventually, microthalli produced erect *Scytosiphon* plants through vegetative development. Crusts were not seen in natural collections that could be related to the erect thalli of either the dwarf or the larger *Scytosiphon* plants, nor were crusts observed in culture material of either popula-

tion. Wynne (1969) demonstrated however, that, as in *P. fascia*, the crust stage of *Scytosiphon* can be induced environmentally.

Dictyosiphon chordaria Aresch.

Collected once, June, 1963, epilithic in the sublittoral. Station 2.

LAMINARIALES

Chorda filum (L.) Stackh.

This species is a strict summer annual at the Ipswich marsh, occurring on rocks and shells in the sublittoral from June through August, and forming sporangia during July and August. Stations 1-2.

Laminaria saccharina (L.) Lamour.

The only species of *Laminaria* in the Ipswich marsh, *L. saccharina*, encompasses two anatomical varieties with respect to the occurrence of mucilage ducts in the stipes and blades of these plants. These varieties, formerly considered as *L. saccharina* and *L. agardhii* (Wilce, 1965), exist throughout the year at Stations 1-2 attached to rock, shell and wooden pilings. Sori with mature sporangia occurred in these populations from late October through March.

FUCALES

Fucus distichus L. emend, Powell ssp. *evanescens* (C. Ag.) Powell

This species, common but not abundant, occurs at Ipswich only at the littoral-sublittoral interface attached to the occasional large rock at Stations 1-2. Plants of this species were reproductive from April to June. As the uppermost vertical extension of *Fucus distichus* coincides with extreme low later level, the occurrence of these plants offers a fairly accurate reference to aid in determining the approximate level of the tide.

Fucus vesiculosus L.

Epilithic in the sublittoral and littoral, reproductive essentially throughout the year, this species constitutes the greater portion of the macroscopic algal vegetation along the Castle Neck River, Stations 1, 2; a few plants occurred at Station 3.

Ascophyllum nodosum (L.) Le Jol.

Plants of *Ascophyllum* occurred in the same habitats and at the same stations as did *Fucus vesiculosus*. This species, however, never developed the luxuriancy or the abundance seen in populations of *F. vesiculosus*. *A. nodosum* could be found reproductive from late November through March.

MARSH FUCOIDS

The marsh fucoids, *Fucus vesiculosus* var. *spiralis* Farl. and *Ascophyllum nodosum*, *f. scorpoides* (Horn.) Reinke constitute a prominent feature of the algal vegetation on the marsh at only one small area of the littoral zone along the Castle Neck River (Station 2). Marsh fucoids undoubtedly occur elsewhere in the broad expanses of the Ipswich Marsh, but they were not otherwise seen in that portion of the marsh represented by our transects.

Plants of both species referred to above are unattached at Station 2 and cover most of the marsh surface in the Spartinetum alternifloretum. These free-living forms or "ecads" of the typical *Fucus vesiculosus* and *Ascophyllum nodosum* are consistently smaller than their attached counterparts, are usually spirally twisted with more numerous branching, and only rarely become reproductive.

Owing to their frequent dense populations in salt marshes, ecads of *Fucus* and *Ascophyllum* represent adaptable tools of research for the phycologist interested in vegetative and reproductive development, and the factors that control these phenomena. Some attempts were made to determine the potential of different ecads to revert to the species habit, but with little success. A more extensive discussion of these plants will be presented in a paper dealing with the ecology of the Ipswich marsh algae.

RHODOPHYTA

For the systematics of the red algae we have followed essentially the treatment used by Taylor (1957); for *Trailliella*, *Antithamnion*, and species of *Ceramium* and *Polysiphonia*, we have relied on Rosenvinge (1909-1931).

BANGIALES

Erythrotrichea carnea (Dillw.) J. Ag.
Epiphytic on *Ceramium*, *Chondrus*, and *Polysiphonia*, July to October. Stations 1, 2.

Goniotrichum alsidii (Zanard.) Howe
Epiphytic on *Ceramium*, *Polysiphonia*, and *Ascophyllum*, July to October, Stations 1-3.

Porphyra umbilicalis (L.) J. Ag.
Epilithic at low tide level, located only in June, 1963. Stations 1, 2.

CRYPTONEMIALES

Dumontia incrassata (O. F. Muell.) Lamour.
Common on rocks in the sublittoral zone, February through May, tetraspores in May. Stations 1, 2.

Hildenbrandia prototypus Nardo
Epilithic at low tide level through the year, tetraspores from July to October. Stations 1, 2.

Gloiosiphonia capillaris (Huds.) Carm. ex Benk.
Sublittoral zone, Castle Neck River, May, 1965, with cystocarps. Station 2.

Euthora cristata (C. Ag.) J. Ag.
Washed ashore during autumn and spring, tetraspores in March. Station 2.

GIGARTINALES

Agardhiella tenera (J. Ag.) Schmitz
Located only during June and July, 1963, the plants vegetative and epilithic in the sublittoral zone. Stations 1, 2.

Gracilaria verrucosa (Huds.) Papenf.
Seen only in June, 1963 and February and October, 1964, epilithic in the sublittoral zone, cystocarps in October. Station 2.

G. foliifera (Forssk.) Børg.
Epilithic in the sublittoral zone through the year, cystocarps in February and July. Station 2.

Chondrus crispus Stackh.
On sublittoral rocks through the year, carpospores from summer to December, tetraspores from December through March. Stations 1-4.

RHODYMENIALES

Halosaccion ramentaceum (L.) J. Ag.

Abundant in the sublittoral zone from June to August, 1963 only, tetraspores always present. Station 2.

CERAMIALES

Trailliella intricata (J. Ag.) Batt.

The Ipswich plants agree with the original description of this species by Batters (1896) and with subsequent descriptions by Rosenvinge (1909-1931) and Taylor (1957). Tetrasporophytes occurred in October, 1964. These collections add to the few reports (Lewis & Taylor, 1928; Taylor, 1941; Chen, et. al., 1969) of *Trailliella* tetrasporangia from northeastern North America. Fully developed sporangia were observed, measuring 68-74 μ wide and 49-53 μ long, and occurring in a linear series.

The occurrence of *Trailliella intricata* was never large and in the Ipswich marsh it was seen only at Station 1. The small sample of tetrasporangia found in October, 1964 is not sufficient for generalizations as to their yearly occurrence in the marsh. It is noteworthy, however, that the date of our collections of tetrasporangia bearing plants coincides with a recorded peak of abundance of these organs from plants in the Northumberland Strait, and the Atlantic Coast of Nova Scotia, Canada (Chen, et. al., 1969).

Antithamnion cruciatum (C. Ag.) Naeg.

Entangled among *Agardhiella*, June, 1963. Station 1.

Ceramium diaphanum (Lightf.) Roth.

Epilithic in the sublittoral zone, June to September, tetraspores in June and July. Station 3.

C. fastigiatum (Roth.) Harv.

Male, female, tetrasporophytes during the year, epilithic in the sublittoral zone, Station 3. Only tetrasporic plants occurred during September and October at Stations 1, 2.

C. rubrum (Huds.) C. Ag.

Epilithic, also epiphytic on *Gracilaria foliifera*, June to November with tetraspores, cystocarpic plants in July and November. Stations 1, 2.

C. rubriforme Kylin
Epilithic in the sublittoral with cystocarps, July to September. Station 2.

Ptilota serrata Kuetz.
Washed ashore in January and March, 1963, tetraspores in March. Station 2.

Phycodrys rubens (L.) Batters
Washed ashore October to March, cystocarps in January, tetraspores in November, January, and March. Station 2.

Polysiphonia flexicaulis (Harv.) Collins
Seen only in June, 1963, epilithic in the sublittoral. Station 3.

P. urceolata (Lightf. ex Dillw.) Grev.
On small stones, July through September, the plants small (to 6 cm), remaining vegetative. Substation 5a.

P. denudata (Dillw.) Grev. ex Harv. in Hook.
Epilithic in the sublittoral zone from July through December, cystocarps from June to October, tetrasporophytes in August. Stations 2, 3.

P. nigra (Huds.) Batt.
Epilithic in the sublittoral, March to October, with male plants in June, female and tetrasporophytes from July to October. Stations 1, 2.

P. lanosa (L.) Tandy
Epiphytic on *Ascophyllum nodosum*, cystocarps in September, Station 1.

Chrysophyta

With the possible exception of some species of *Vaucheria*, most recently studied in our area by Blum & Conover (1953), Blum & Wilce (1958), Blum, 1960 and Webber (1968), the salt marsh representative of the classes Xanthophyceae, Dinophyceae, Chrysophyceae and Haptophyceae in North America are poorly understood. We wish to emphasize that most members of these taxa are inconspicuous elements of the cold season salt marsh vegetation, and they represent (especially species of benthic Chrysophyceae and Haptophyceae) a little known area of study for the laboratory or field oriented phycologist.

Data as to the occurrence, seasonal and reproductive periodicities, and life history details of salt marsh members of the above classes are wanting for most. By far the largest number of species have only their occurrence listed for a single or several locations in North America. Experimental research efforts with representatives of these taxa have been initiated recently (e.g., Park, 1961; Boney & Burrows, 1966; Boney 1967). However, many marine species either new to science or previously unknown in North America undoubtedly remain to be described; virtually all of the biology of these species lies in the unknown.

The main references used for the Xanthophyceae (Vaucheriales) were Blum and Conover (1953) and Taylor (1957). Systematic treatments of the remaining classes follows Parke (in Parke and Dixon, 1964).

XANTHOPHYCEAE (Vaucheriales[3])

Vaucheria compacta (Collins) Collins var. *koksoakensis* Blum & Wilce

Conspicuous from May through November carpeting the mud of creek banks, reproductive from July to December. Substation 5a.

V. arcassonensis Dangeard

Forming mat-like expanses in the soil at the bases of *Spartina patens*, reproductive plants located in May, vegetative material apparent from June through August. Station 2.

V. intermedia Nord.

Located in the mud at seaward edges of the marsh, and mixed with *Vaucheria arcassonensis*, the plants reproductive from September through the winter to March, then vegetative and most abundantly so in June and July. Stations 1, 2.

DINOPHYCEAE (Phytodiniales)

Urococcus foslieanus Hansgr.

With *Ruttnera*, this species is an important constituent of the winter microvegetation. *Urococcus* was first lo-

[3]See Webber, 1968.

cated in quantity in *Spartina* debris, where a few isolated cells persisted through the summer. Daughter cell formation was observed in September, 1962 and in January, 1964, but release of these cells was not seen, even after prolonged observation.

CHRYSOPHYCEAE (Ochromonadales)

Ruttnera maritima (Anand) Parke

Plants unicellular, aggregated, with a thick gelatinous matrix, each cell with a parietal chromatophore, numerous oil droplets, and upon several occasions a pyrenoid was observed in each cell.

This species was first located in early November from soil beneath the *Spartina* grasses and from old culms of these plants. At Ipswich, *Ruttnera* was most abundant from January through March, with the populations persisting to early June. The quantities of oil droplets increased and the chromatophore became more diffuse as June approached. Formation and discharge of motile cells was seen from field collections of February, 1964; each cell produced 8 daughter cells which, upon release, showed no evidence of fusion. Under culture conditions of 14°C and 100 f.c. of light, these swarmers grew into small branched filaments floating at the surface of the culture solution. Further attempts to study the continued development of these filaments was unsuccessful.

Anand's (1937a, b) *Ruttnera* species were distinguished by the presence (= *Gloeochrysis maritima* Anand) or absence (= *Gloeochrysis littoralis* Anand) of a pyrenoid. Pyrenoid occurrence in *Ruttnera* cells at Ipswich seems to be variable as observed with the aid of a light microscope. Further, the degree of stratification of the cells' matrix, a species criterion also used by Anand, seems to be ecologically controlled.

It is our opinion that there is insufficient evidence now that these characteristics are valid species criteria. Until additional cytological and morphological data are available, we consider the Ipswich plants as *Ruttnera* sp., with the closest affinity to *R. maritima*.

HAPTOPHYCEAE (Phaeothamniales)

Material of this family representing a new genus will be treated in more detail in a later publication.

Plants filamentous, branching, the branches entangled, cells 6-7 μ diam. and 12-18 (28 μ long, constricted at the septa, chromatophores parietal and band-shaped, 1-3 per cell, lacking pyrenoids.

Of common occurrence in the leeward face of wood pilings in the marsh sublittoral, especially so from early October through the winter to late May.

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GREENMANIA: A TAXONOMIC SYNONYM OF UNXIA (COMPOSITAE: HELIANTHEAE)

TOD F. STUESSY[1]

Greenmania and the type species, *G. boladorensis*, were described in 1901 by Georg Hieronymus from material collected by P. Sonntag (*51*) "in monte Bolador" during August of 1881 in Colombia, South America. In 1907 Hieronymus described a second new species in the genus, *G. ulei*, this time from a specimen collected by E. Ule (*5146*) on 29 July 1900 "an feuchten Stellen bei Manaes" in Amazonian Brazil. Examination of the fragments and photographs of the type specimens of these two species in the U. S. National Herbarium has shown that *Greenmania* is congeneric with *Unxia* L.f., a genus recently re-established in the subtribe Melampodiinae and also found throughout the northern regions of South America (Stuessy, 1970). S. F. Blake many years ago perceived the congeneric relationship of these two taxa as evidenced by his handwritten note placed inside the packet containing fragments of the type of *G. ulei*, in which he stated that the species is "a genuine congener of *M*[*elampodium*] *camphoratum*" [=*Unxia camphorata*].

Greenmania thus becomes a taxonomic synonym of *Unxia* (validly published in 1781), and *G. boladorensis* and *G.*

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